Evolutionary Graph Theory Fixation times on directed graphs

David Brewster

Harvard University

Joint work w/ Martin Nowak and Josef Tkadlec

Evolutionary graph theory

How does stuff propagate through networks?

Maximizing the spread of influence through a social network

[HTML] Evolutionary dynamics on graphs

E Lieberman, C Hauert, MA Nowak - Nature, 2005 - nature.com

... Here we introduce evolutionary graph theory, which suggests a promising new lead in the effort to provide a general account of how population structure affects evolutionary dynamics.... ¢ Save 99 Cite Cited by 1379 Related articles All 44 versions

(HTML) Complex networks: Structure and dynamics <u>S Boccaldu</u>, <u>V Latora</u>, <u>V Moreno</u>, M Chavez... Physics reports, 2006 - Elsevier Coupled biological and chemical systems, neural networks, social interacting species, the Internet and the World Wide Web, are only a few examples of systems composed by a large ...

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Statistical physics of social dynamics

<u>C Castellano, S Fortunato, V Loreto</u> - Reviews of modern physics, 2009 - APS ...best to mention relevant social science filterature and highlight connections to it, the main focus of this work remains a description of the statistical physics approach to social dynamics... of Save 95 Cite Cited by 4214 Related articles All 28 versions

(HTML) Evolutionary games on graphs

G Szabó, G Fath - Physics reports, 2007 - Elsevier

Game theory is one of the key paradigms behind many scientific disciplines from biology to behavioral sciences to economics. In its evolutionary form and especially when the ... $\frac{1}{\sqrt{2}}$ Save 99 Cite Cited by 2729 Related articles All 18 versions

[HTML] Statistical physics of human cooperation

<u>M Perc, JJ Jordan, DG Rand, Z Wang, S Boccaletti...</u> - Physics Reports, 2017 - Elsevier ...the relevance of physics in all of this. Methods of statistical physics have recently been ... Statistical physics of social dynamics [13], of evolutionary games in structured populations [... ¢ Save 99 Cite Cited by 918 Related articles. All 8 versions

coronavirus among humans

- influence (opinion, gossip, fake news) on social media
- genetic mutation in a population of individual organisms

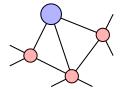
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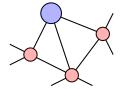
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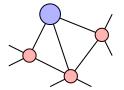
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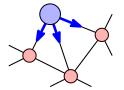
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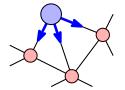
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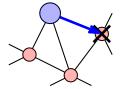
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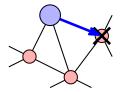
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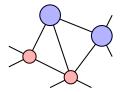
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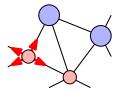
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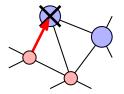
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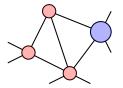
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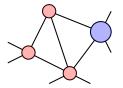
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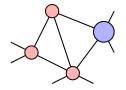
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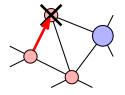
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	fitness
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- 1. It is stochastic (random).
- 2. In some steps, nothing happens.
- 3. Nodes can toggle back and forth (more opinions than gossip).
- 4. Eventually, all nodes become the same type (no mutation).
- 5. Variants exist (e.g. death-Birth updating).

- 1. Fixation probability $fp^r(G)$: Average probability that, starting from a single node, mutants spread to all sites.
- 2. Fixation time $T^{r}(G)$: Average time until one type wins.
 - Measured in steps or better in generations.

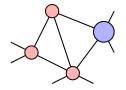


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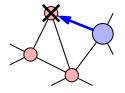
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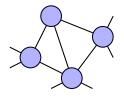


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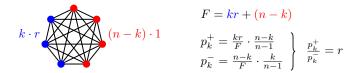


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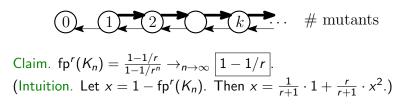
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Special case: Complete graph K_n and r > 1



It turns out that we are always r-times more likely to gain than to lose a mutant. Thus the process can be mapped to a 1-dimensional random walk, with a constant forward bias r.

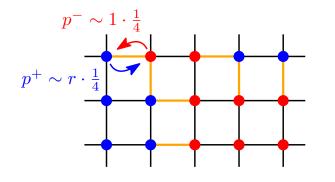


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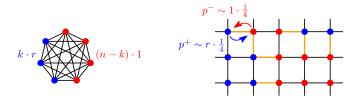
Special case: Regular graphs R_n Claim (Isothermal theorem, '05). For any regular graph we have

$$\operatorname{fp}^r(R_n) = \operatorname{fp}^r(K_n).$$

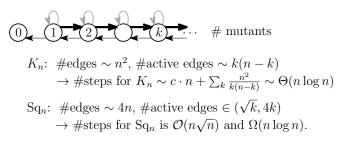
Proof. The same mapping works! We say that an edge is active if its endpoints are of different types. Each active edge is r-times more likely to be used in gaining rather than losing a mutant.



But #steps on regular graphs differ



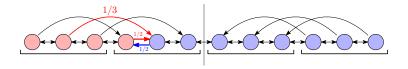
Intuition. If a of E edges are active, then, on average, roughly one in every E/a steps is active.

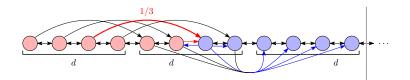


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Simulations can be slow on directed graphs





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[B-Nowak-Tkadlec '23+]



[B-Nowak-Tkadlec '23+]

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[B-Nowak-Tkadlec '23+]

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- 2. If graph is *Eulerian* and *r* is slightly larger than ratio between max degree and min degree, fixation occurs quickly.

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3. For some graphs (even undirected), increasing mutant advantage can result in longer fixation times.

[B-Nowak-Tkadlec '23+]

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Balanced graphs

[B-Nowak-Tkadlec '23+]

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$$\frac{1}{\deg^{-}(v)} \cdot \sum_{u: u \to v \in E} \frac{1}{\deg^{+}(u)} = \frac{1}{\deg^{+}(v)} \cdot \sum_{w: v \to w \in E} \frac{1}{\deg^{-}(w)}$$

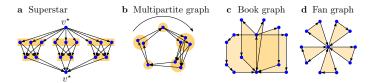
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Games on directed graphs

- Directed graph G = (V, E)
- death-Birth updating
- Given death node $v \in V$, fitness of $u \in \Gamma^-(v)$ is 1 w + wPwhere P is total payoff from playing games with nodes in $\Gamma^-(v)$

	Mutant	Resident
Mutant	r	r
Resident	1	1
	Cooperate Defect	
Cooperate	b – c	- <i>C</i>
Defect	b	0

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for r > 1 and b > c > 0.

References I



Philipp M. Altrock, Chaitanya S. Gokhale, and Arne Traulsen.

Stochastic slowdown in evolutionary processes. Physical Review E, 82(1):011925, July 2010.



Benjamin Allen and Martin A. Nowak.

Games on graphs. EMS Surveys in Mathematical Sciences, 1(1):113–151, April 2014.



Josep Díaz, Leslie Ann Goldberg, George B Mertzios, David Richerby, Maria Serna, and Paul G Spirakis. Approximating fixation probabilities in the generalized moran process. Algorithmica, 69:78–91, 2014.

▲□▶ ▲□▶ ▲□▶ ▲□▶ □ のQで



Josep Díaz, Leslie Ann Goldberg, David Richerby, and Maria Serna.

Absorption time of the moran process. Random Structures & Algorithms, 49(1):137–159, 2016.



Andreas Galanis, Andreas Göbel, Leslie Ann Goldberg, John Lapinskas, and David Richerby. Amplifiers for the moran process. Journal of the ACM (JACM), 64(1):1–90, 2017.



Rasmus Ibsen-Jensen, Krishnendu Chatterjee, and Martin A Nowak. Computational complexity of ecological and evolutionary spatial dynamics. Proceedings of the National Academy of Sciences, 112(51):15636–15641, 2015.



Travis Monk, Peter Green, and Mike Paulin.

Martingales and fixation probabilities of evolutionary graphs. Proceedings of the Royal Society A: Mathematical, Physical and Engineering Sciences, 470(2165):20130730, 2014.

References II

Patrick Alfred Pierce Moran.

Random processes in genetics.

In <u>Mathematical proceedings of the cambridge philosophical society</u>, volume 54, pages 60–71. Cambridge University Press, 1958.

▲□▶ ▲□▶ ▲□▶ ▲□▶ □ のQで



Martin A Nowak.

Evolutionary dynamics: exploring the equations of life. Harvard University Press, 2006.



Josef Tkadlec, Andreas Pavlogiannis, Krishnendu Chatterjee, and Martin A Nowak. Population structure determines the tradeoff between fixation probability and fixation time. Communications biology, 2(1):138, 2019.



Josef Tkadlec, Andreas Pavlogiannis, Krishnendu Chatterjee, and Martin A Nowak. Limits on amplifiers of natural selection under death-birth updating. PLoS computational biology, 16(1):e1007494, 2020.



Josef Tkadlec, Andreas Pavlogiannis, Krishnendu Chatterjee, and Martin A Nowak. Fast and strong amplifiers of natural selection. Nature Communications, 12(1):4009, 2021.

Questions?

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